THE DEVELOPMENT OF THE ASYMMETRICAL WEB OF *NEPHILENGYS CRUENTATA* (FABRICIUS)

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Edmunds, J. 1993 11 11: The development of the asymmetrical web of *Nephilengys cruentata* (Fabricius). *Memoirs of the Queensland Museum* 33(2): 503-506. Brisbane. ISSN 0079-8835.

In the field, young *Nephilengys cruentata* (Fabricius) remain on the barrier threads of their mother's web for about ten days, before moulting. Some do not initially disperse far, and may even remain on the barrier threads to build their first web. These first webs are complete orbs. As the spiderlings grow the hub of the web is spun approximately three quarters of the way up the web; later there are no spirals above the hub. At this stage some spiders join the hub to the barrier, forming a 'tent' under which the spider rests. The true retreat, of a tube that is closed at the end away from the hub, develops gradually as the spiders grow further.□*Nephilengys, web development, evolution of webs.*

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Nephilengys cruentata (Fabricius) is common throughout tropical Africa. In Ghana it lives in savanna and forest edge areas. Under natural conditions it attaches its web to trees, but it has frequently adapted to attaching it to dwellings. It was very common at Legon in such situations. The adult female is large but the male is much smaller. The webs of larger spiders are usually a roughly triangular partial orb. The hub is at the upper apex, where there is a cylindrical retreat, closed at the end away from the hub. There is an extensive barrier above and behind the viscid web; the main attachment between the two is at the hub. The hub and retreat are often in the angle between a wall and the ceiling or overhang. This paper presents data on the shape of the web of *N. cruentata* from the earliest instars to adults.

METHODS

Spiders of all ages were observed living on the verandahs of a private dwelling and of the Zoology Department at Legon, but it was not possible to follow individual spiders in the field or captivity. Web size and length of the first leg of each spider were measured, although the relation between spider size and instars was not determined. The vertical asymmetry, lateral asymmetry and shape (circularity) of the web were determined from the ratios of vertical radii, horizontal radii and the two diameters respectively, all measured to the nearest 5mm; N for all figs is given in Table 1.

RESULTS

The cocoon is laid close to the web, often on a wall or ceiling. When the spiderlings emerge, they remain close to where they have emerged in a tight bunch on the barrier web for about ten days, spinning extra irregular threads. After the first post emergence moult, they disperse, but many remain close to the mother's web, some even building their first catching web in the threads of the barrier web.

When the spiders are grouped into different size classes based on leg 1 length, the extent of the web below the hub increases with each succes-

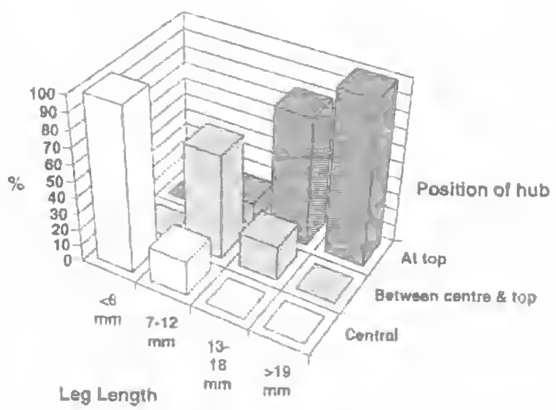

FIG. 1. Changes in vertical asymmetry in webs of *N. cruentata* with different leg lengths. At top: ratio of upper to lower radius = 0; Between centre and top: ratio of upper to lower radius >0 <1; Central: ratio of upper to lower radius = 1 .

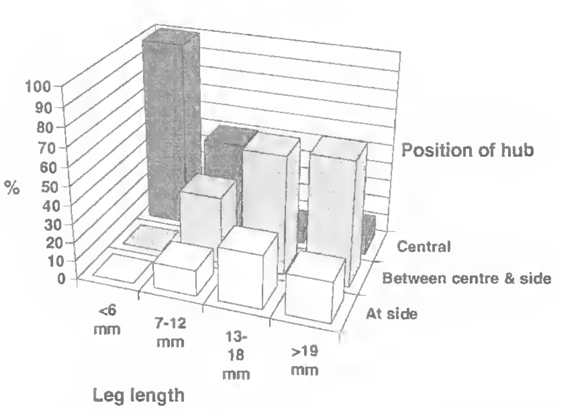

FIG. 2. Changes in lateral asymmetry in webs of *N. cruentata* with different leg lengths. At side: ratio of two horizontal radii = 0; Between centre and side: ratio of two horizontal radii >0 <1; Central: ratio of two horizontal radii = 1.

sive class, while that above the hub increases slightly before decreasing to zero (Table 1).

The vertical asymmetry increases with size (Fig. 1): spiders with leg 1 <6mm spin complete orbs. As they grow, less web is spun above the hub, so that the hub is then about three quarters of the way up the web. Larger spiders, with leg 1 >19mm have no web above the hub. Because of the difficulty in following individual spiders, the time span over which these web changes occurred is not known.

Early webs are symmetrical laterally (Fig. 2), but webs of larger spiders show greater variation and may be markedly asymmetrical laterally; at the extreme the hub is completely to one side. Some early webs are also circular or nearly so (Fig. 3), however very few webs of spiders with leg 1 > 6mm have the vertical and horizontal diameters of the same size.

During these changes in the proportions of the

TABLE 1. Body size and web dimensions (in mm) in different size classes (based on leg 1 length) of *Nephilengys cruentata*.

Leg 1 length	<6	7-12	12-18	>19
Body size	<3.5	3.5-7.0	7.0-9.0	>9.0
N	8	14	14	9
Hub-web top:mean	38.1	47.1	19.2	0
range	25-50	0-80	0-100	0
Hub-web bottom: mean	38.1	109.3	180.0	478.9
range	25-50	45-170	140-260	200-700
Web Width: mean	73.8	117.9	177.4	431.1
range	70-90	80-180	80-290	240-850

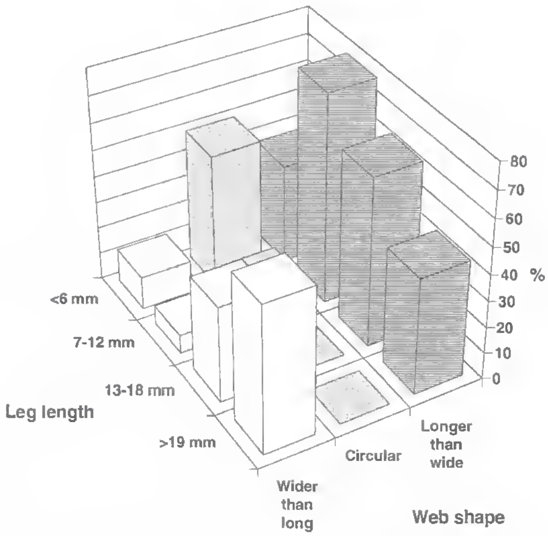

FIG. 3. Changes in shape in webs of *N. cruentata* with different leg lengths. Longer than wide: vertical diameter > horizontal diameter; Central: vertical diameter = horizontal diameter; Wider than long: vertical diameter < horizontal diameter.

viscid web, the barrier increases (Fig. 4). The very first webs have no barrier or just a few threads, which are attached to the orb at only a few points. But over some days more threads are added, until the barrier is a fairly dense cone shaped tangle behind the orb, and more firmly fixed to the web. Small pellets of detritus, similar in size and shape to the spiderling and of the same pale grey colour, usually occur in the barrier (Edmunds and Edmunds, 1986). These may deflect attacks of potential predators.

The development of the retreat increases with the size of the spider (Fig. 5). Spiders with the hub

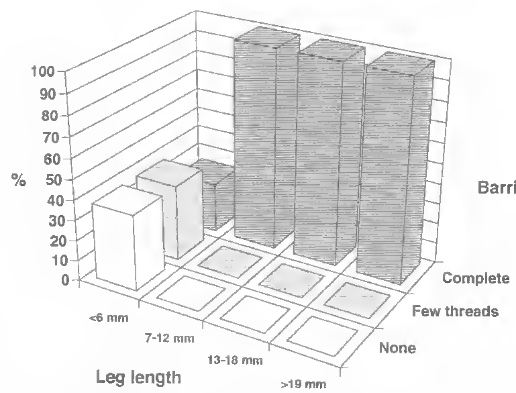

FIG. 4. Development of barrier in webs of *N. cruentata* with different leg lengths.

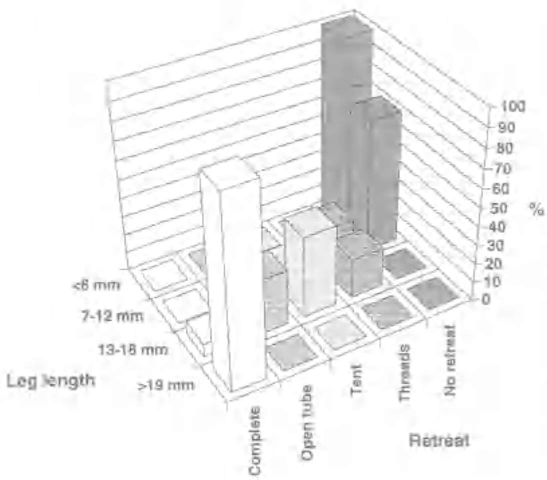

FIG. 5. Development of retreat in webs of *N. cruentata* with different leg lengths.

at the centre or part of the way up the web rest at the web hub and there is no retreat. When the hub is built at or very close to the apex, the first stages of a retreat are formed as a denser group of threads within the barrier close to the hub. As more threads are added, this becomes a roof-like tent between the hub and the barrier, or sometimes an open ended tube. Spiders with leg 1 >19mm normally had a closed tubular retreat, like an adult.

Early webs are very fine, and it is not easy to see the details of the individual threads. However, a complete web appears to be spun in one operation, unlike larger webs which are spun in two or more sections on different days. The temporary spiral does not appear to be left up, though more detailed observations would be needed to confirm this. Larger spiders leave the temporary spiral in the finished web.

DISCUSSION

The webs of most adult female Nephilinae are not typical orbs. Most *Nephila* species build incomplete orbs, with the hub near the top (Robinson and Robinson, 1973, figs 2, 20; pers. obs.). However, unlike *Nephilengys*, there are threads above the hub, including in some instances a few sticky spirals. In *Nephila plumipes* large, probably mature, females were seen in Brisbane, Australia, that had several sticky radii above the hub. However, in at least some individuals, these appeared to have been laid as pendulum turns, rather than complete spirals (pers. obs.). *Nephila* does not build a retreat and the spider rests at the hub. Like *Nephilengys*, there are barrier webs, though on both sides, and often above the orb. These are supportive and probably also defensive (Robinson and Robinson, 1973). *Herennia ornatissima* (Doleschall) constructs a very long web, with almost parallel sides (Robinson and Lubin, 1979). The spider sits in a cup-shaped depression of dense silk that forms the hub. It is towards the top of the web, though there are several sticky spirals above it. The spider has no barrier web, but as it builds very close to tree trunks, it would be difficult to find a place to build one.

Larger juvenile Nephilinae build webs like the adults, and a few observations have been published on the very early webs. The first webs of *Nephila clavipes* (Linnaeus) are circular (Comstock, 1948; Levi and Levi, 1968). Brown and Christenson (1983) give measurements of the webs of *N. clavipes* spiderlings between 2 and 9mm body length. The webs show an increase in vertical asymmetry as they grow. However, unlike *Nephilengys cruentata*, even the instars that spin the first catching webs had the hub approximately two thirds of the way up the web. Both species seem to spin the hub at the top of the web when they reach a similar size. Webs with spirals above the hub are spun by juvenile *Nephila maculata* (Fabricius) (Robinson and Robinson, 1973, figs 5, 6), and possibly by *Nephila senegalensis* (Walckenaer) (Clausen, 1987). The webs of juvenile *Herennia ornatissima* (Robinson and Lubin, 1979) are also more like a complete orb.

The fact that the earliest webs of at least some species of Nephilinae are complete orbs indicates that the orb is a primitive characteristic in them, and that the incomplete orbs of the larger spiders are derived. There are other spiders which have a highly modified orb-web, but build a more complete orb as a juvenile. Spiders of the genus *Scoloderus* build extremely elongated inverted ladder webs, with the hub towards the base. The juveniles of *Scoloderus tuberculifer* O.P.-Cambridge have webs that are far less distorted (Eberhard, 1975). However, even the smallest *S. cordata* (Taczanowski) have elongated ladders (Stowe, 1978). In *Araneus atrihastulus* from New Zealand, which builds a web that is elongated both above and below the hub, some of the proportions of juvenile webs are less extreme (Forster and Forster, 1985). It would be interesting to find the very early webs of other spiders with atypical webs, such as that of the spider that built the ladder web observed by Robinson and

Robinson (1972) in New Guinea, now identified as close to *Tylorida* (Eberhard, 1990b). Other aspects of web construction and use may be more derived in adults than in juveniles, such as the angle of the spring line and resting position of the spider in *Epeirotypus* sp. from Costa Rica (Eberhard, 1986). However, in the west African *Pararaneus cyrtoscapus* (Pocock), the conical horizontal webs of juveniles are more derived than the planar vertical of adult females (Edmunds, 1978).

If it is confirmed that young *Nephilengys cruentata* build webs in one piece and destroy temporary spirals, then the adult behaviour of leaving the temporary spirals in place is presumably also a secondary modification. There are other characteristics of the webs of Nephilinae that are derived. Despite their size, the webs of adults have a finer mesh compared to some other orb weavers (personal observation). Eberhard (1982, 1990a) concludes that some characteristics of the web building behaviour of *Nephila clavipes*, such as the unique method of laying the sticky spiral, are an adaptation to spinning a tightly meshed web, even though other aspects (e.g. frame construction) are primitive. Levi (1986), Eberhard (1990a) and Coddington (1990) classify the Nephilinae with the Metinae and tetragnathids, rather than with *Araneus* and its relatives. The derived nature of the partial orb of the larger Nephilinae would be consistent with this classification.

ACKNOWLEDGEMENTS

I would like to thank Prof D.W. Ewer for the use of facilities while working at the University of Ghana, and Malcolm Edmunds for constructive comments.

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